

ATTENDANCE LEVELS AND BEHAVIOUR AT BOWERS BY MALE GOLDEN
BOWERBIRDS, *PRIONODURA NEWTONIANA* (PTILONORHYNCHIDAE)

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Attendance levels, bower maintenance, and behaviour of male Golden Bowerbirds *Prionodura newtoniana* at their bower sites were studied over the display seasons of 1982 and 1983 in 50ha of upland rainforest. The display season typically started in late August/early September and terminated in December/January when wet season rains commenced, but its length varied year to year apparently in response to climate and/or food availability. During season 1982 males spent an average of 36% of daylight at their bowers; at a mean of 2.7 visits per hour, and each visit averaging 8mins. During season 1983, males spent longer at bowers (mean = 63%); at a mean of 3.4 visits per hour, and each visit averaging 11mins. Lower attendance in 1982 involved all males during each month and different times of the day, and was attributed to excessively dry conditions; bower activity ceased by early December. Males spent on average 6% of their time at bower sites giving advertisement song, 8% other calls, 4% maintaining bowers, 2% displacement chasing and displaying, and the remaining 80% perched silently above their bower. Vocalisations were given from habitually-used, mostly horizontal (99%), perches averaging 9.3m from the bower perch and 5.6m above ground. Advertisement song consisted of a prolonged, pulsating *rattle* repeated an average of nine times, with each series averaging 33secs. Other calls included *squeals*, *screeches*, *wolf-whistles*, *scolds*, frog- and cicada-like notes, given as single notes or as a medley with fine vocal avian mimicry of at least 22 model species. Most (95%) bower decorations were collected away from the bower site; having been harvested, or stolen from a neighbouring rival's bower. Others were retrieved from a 'store' near the bower, where they had been left previously. Intruding rival bower-owners managed to steal a decoration on 83% of their visits, obviously being most successful (100%) in the owner's absence. Of 144 displacement chases of birds from a bower/bower site, 76% were directed at conspecifics and 24% at other birds (at least seven spp.). Males instantly displaced and chased off conspecific visitors (79%), mostly from the bower perch. Males were seen to display to a female-plumaged individual 26 times, 20 times being before/after displacement chases. Three display elements were performed by males at bower sites: *Bow*, *Head nod and Shake*, and *Flight/hover*. A total of 146 displays consisted of one ($n = 78$), or a combination of ($n = 68$), these elements, and an element was often repeated more than once during a display; there being no apparent sequence of elements. Copulation was not witnessed. □ *Golden Bowerbird, Prionodura newtoniana, Ptilonorhynchidae, bower attendance, time budgets, behaviour, vocalisations.*

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Until recently the Golden Bowerbird *Prionodura newtoniana* remained one of the least studied of bowerbirds. The first quantitative studies of its nesting biology, dispersion and constancy of bower sites, variation and seasonal changes in bower structures, home ranges and associated sociobiology and ecology have only recently appeared (Frith & Frith, 1998, 2000a, 2000b). Male attendance levels at bowers have been examined in other bowerbird species (Veselovsky, 1978; Donaghey, 1981; Pruett-Jones & Pruett-Jones, 1982, 1985; Frith & Frith, 1994; Lenz, 1993), but until this study no such data were available for Golden Bowerbirds. Previous

contributions provide qualitative casual observations of male bower attendance and behaviour, but no quantitative data (Bourke & Austin, 1947; Marshall, 1954; Chisholm & Chaffer, 1956; Warham, 1962; Chaffer, 1984).

The display season and male attendance of the Golden Bowerbird starts in late August/early September with bower-owners giving loud, prolonged, rattle-like advertisement song above traditional bowers, adding fresh sticks, and placing decorations upon them (Frith, 1989; Frith & Frith, 2000a,b). Other bower calls include squeals, screeches, croaks, rasps and churrings (Schodde & Tideman, 1988; Frith, 1989;

Donaghey, 1996). Males also produce fine vocal avian mimicry, as do other bowerbird species (Loffredo & Borgia, 1986; Frith & Frith, 1990a,b; 1993; 1994; Frith & McGuire, 1996; Frith et al., 1996). All individually known bowerbirds regularly attending and vocalising at bowers have proved to be male (Marshall, 1954; Vellenga, 1980; Gilliard, 1969; Cooper & Forshaw, 1977; Frith & Frith, 1993).

Male Golden Bowerbirds spend most time at their bower site perched silently above and around their bowers, the remaining time being spent in calling, displaying, and maintaining and/or decorating the bower (Frith, 1989). The bower consists typically of one or two roughly conical towers of accumulated sticks constructed around one or several supporting saplings and/or small trees, a perch protruding from single towers or connecting twin tower bowers (Frith & Frith, 2000a). Where tower sticks meet the bower perch they are more skilfully placed and aligned to form a discrete 'platform' where bower decorations are exclusively placed. Frith & Frith (2000a) considered the platform(s) the most significant part of the bower structure. For further introduction, and details of structures and dispersion, see Frith & Frith (2000a).

Males display on their bower perch by bowing and nodding, with drooped wings, sometimes with a bower decoration held in the bill. They also display by flying and hovering around the immediate bower area (bower site), thus dramatically emphasising their brilliant yellow plumage (Chisholm & Chaffer, 1956; Chaffer, 1958, 1984; Schodde & Tidemann, 1988). Copulation has not been observed, and may occur on or close to the bower. Males leave their bower site to forage, bathe, collect new bower sticks and harvest, or steal, decorations. That male bowerbirds steal decorations from the bowers of rivals, with a preference for particular colours and items, has long been known (Marshall, 1954 and references therein), but has been only briefly alluded to with respect to Golden Bowerbirds (Frith, 1989). It has been described for several bowerbird species (Borgia, 1985b,c, 1986; Borgia & Gore, 1986; Pruett-Jones & Pruett-Jones, 1994; Frith & Frith 1993, 1994, 1995; Hunter & Dwyer, 1997).

In this contribution, we initially define and describe seasonality of bower attendance over the first three display seasons of our study (1978-80) in relation to rainfall, temperature and fruit and insect food availability. However, most data

presented here deal with bower site attendance levels of males over two display seasons (1982-83), diurnal, monthly and seasonal variations in these, and behaviour and vocalisations at the bower. We discuss these results in the context of knowledge of this and other bowerbirds.

METHODS

STUDY AREA AND CLIMATE. The main study area comprised 50ha of upland tropical rainforest, at about 875m asl, on the Paluma Range (19°00'S, 146°10'E), northeastern Queensland, 7km from Paluma Township and 80km north of Townsville. This area, measuring 1 × 0.5km, was permanently gridded with metal stakes (see Frith & Frith, 2000a: fig. 2). The rainforest has been classified as simple notophyll vine forest (Traey, 1982).

Annual rainfall and temperature show marked seasonality on the Paluma Range (Frith, 1984; Frith & Frith, 1985, 1994; D. Frith & C. Frith, 1990). The dry season extends from April-November, with June-August the driest and coldest months. Rainfall and temperatures increase during September-October and decrease during April-May. The hotter wet season is from December-March, with most rain falling during January-March.

DEFINITIONS. Bower site describes the location of a traditional bower; regularly attended, maintained and decorated throughout each season by the traditional adult male owner (Frith & Frith, 2000a). A traditional bower owner was an individually-marked (colour-banded), bower-attending, bird known to have attend a particular bower during at least one previous season(s). Male attendance refers to known individual males perching, calling, displaying at or maintaining their own bower. Thus a male visiting the bower of another to steal a decoration was not attending it. As we could see only the male bower-owner during most displays we refer to them as 'displays', as distinct from 'courtship displays' (i.e. display directed at a conspecific). We use 'regularly attended' to imply full-time seasonal attendance by traditional owners at traditional bower sites, and write about males unless stated otherwise. To 'harvest' a bower decoration was to obtain it from a plant or the forest floor, as distinct from stealing it from the bower of a rival male. We refer to a display season by the year in which it started (S78, S79 etc).

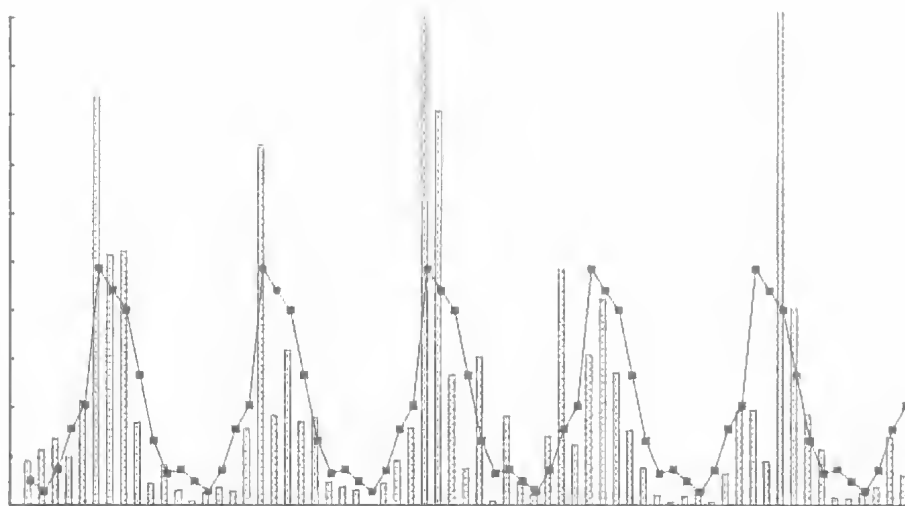


FIG. 1. Monthly rainfall (= columns) from August 1978-December 1983, incorporating five display seasons (S78-S83), and monthly averages for 1978-1990 (= ■) on the Paluma Range, north Queensland.

ANNUAL SEASONALITY OF BOWER ATTENDANCE BY MALES. Seasonality of bower attendance was assessed during S78-S81 by (a) estimating numbers of bower decorations on bowers at our visits (see Frith & Frith, 2000a,b) and subjectively categorising them as being poorly (<10 decorations), moderately (10-20) or well (>20) decorated; (b) noting how many times we heard advertisement songs at traditional bower sites during 280h of transect foraging walks from August 1979 to February 1981; and (c) collecting defaecated seeds on black mesh catchment traps suspended beneath favoured perches above or adjacent to, up to ten, bowers at regular intervals during December 1978-May 1979 and September 1979-February 1981.

Seasonality of bower attendance during S78-S81 was examined in relation to rainfall (Fig. 1), temperature, relative fruit crop and insect numbers (Fig. 2). We collected tree fruiting phenology data from 602 trees during September 1978-April 1979, and thereafter about 500 of these trees were examined at six- (July 1979-August 1980) or eight- (November 1980-February 1981) weekly intervals (Frith & Frith 1985, 1994). Diurnal insect populations were monitored each month from August 1978-April 1979, and July 1979-February 1981, using Malaise traps (Frith & Frith, 1985). We present here the mean diurnal number of all insects trapped per month, and for Coleoptera separately because 80% of any animals remains

found in faecal samples during August 1978-February 1981 were coleopteran (Frith & Frith, unpubl. data).

MALE BOWER ATTENDANCE LEVELS. Male bower attendance levels were monitored during the peak display period of 7 September-15 November 1982. Season 82 was exceptionally dry and bower attendance decreased considerably by early November. We therefore repeated observations the following season, during 3 November-5 December, when rainfall was only just below average, and bowers were regularly attended. Observations over two seasons provided comparative data on seasonal, monthly and diurnal variations.

Six adjacent bowers were monitored during both seasons (bowers 1, 2, 3, 4, 19 and 20; see Frith & Frith, 2000a: fig. 2). We established cryptic canvas hides six metres from each bower two weeks before starting observations. Each observation lasted six uninterrupted hours, during 0600-1200 or 1200-1800h, over peak seasonal activity. Each cycle of observations consisted of two (at 0600-1200h and at 1200-1800h) periods at each of the six bowers (thus 12×6 h observations). When a cycle was completed we repeated it. Observation periods at three sets of two adjacent bowers (bowers 1 and 3 at 260m apart; 2 and 4 at 210m apart; 19 and 20 at 130m apart) were made simultaneously by us, DWF in one hide and CBF in another. During S82 we made 150, 147 and 72h of direct observation

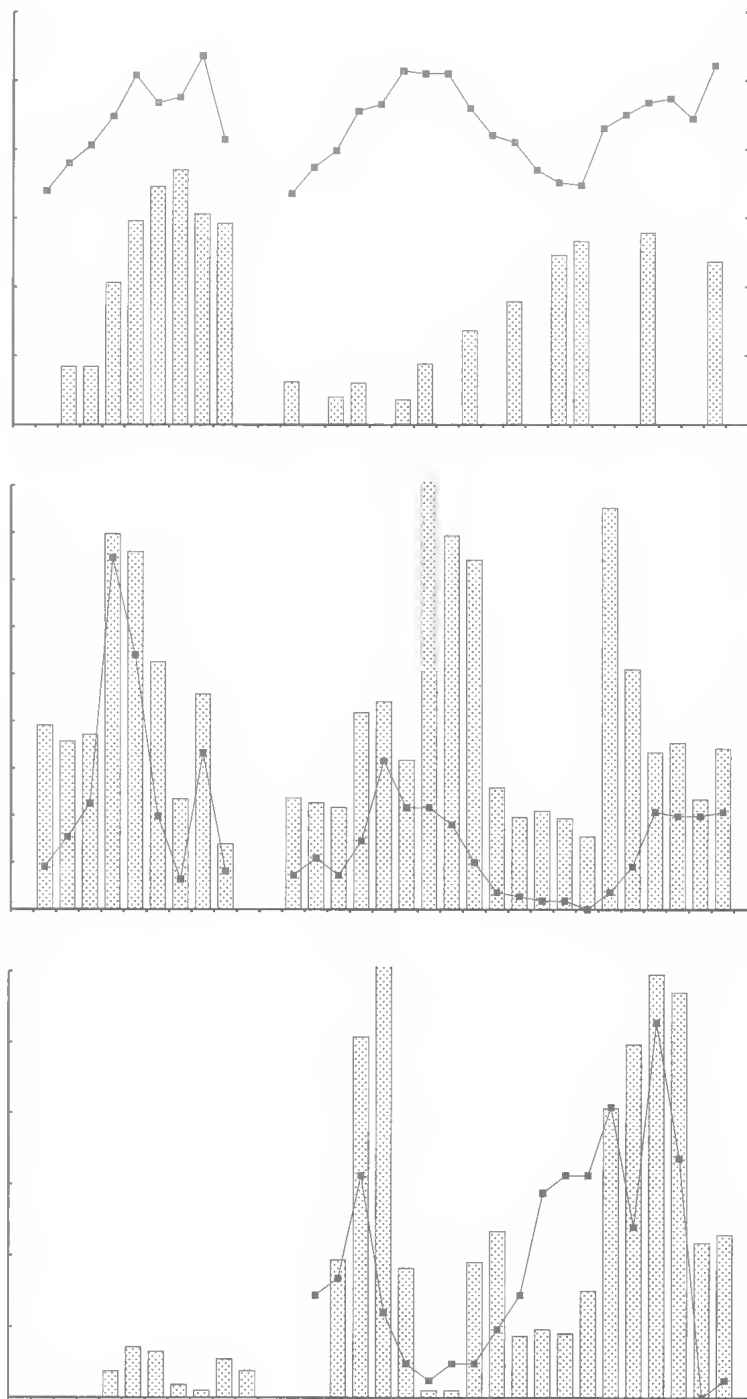


FIG. 2. A, mean monthly temperatures (= ■) and percentages of trees (= columns) sampled monthly that were in fruit. B, mean monthly numbers of all diurnal insects (= columns) and of only Coleoptera (= ■) sampled by Malaise traps. C, mean monthly numbers of defaecated seeds (= columns) collected beneath Golden Bowerbird singing perches and the number of advertisement songs (= ■) heard during track transect walks (see Methods), from August 1978–February 1981 and incorporating three display seasons (S78–S80), on the Paluma Range, N Queensland.

TABLE 1. Bower site attendance levels by individual male Golden Bowerbirds during the display seasons of 1982 (September, October and November) and 1983 (November). * = minimum number for males at bowers 2, 4, 19 and 20 who may have been at that site pre-S78; ** = immature plumage in season 82, adult plumage in season 83; *** = a different adult male regularly attended this bower site during the first two September watches; **** = a different adult male each season; see Methods.

Season	Bower site number	Number of seasons owned *	Hours and (numbers) of observations	Absence		Presence	
				Mean mins per absence	% of total time absent	Mean mins per presence	% of total time present
1982	1	5	46 (8)	12.1	67.9	5.9	32.1
	2	5	60 (10)	13.8	67.1	6.9	32.9
	3**	1	60 (10)	16.2	66.4	8.6	33.6
	4***	5	60 (10)	11.6	53.0	10.4	47.0
	19****	5	66 (12)	13.0	63.5	7.6	36.5
	20	5	63 (11)	17.3	66.9	9.1	33.1
	Total/Mean/%		357 (61)	13.9	64.0	8.0	36.0
1983	1	6	12 (2)	7.8	47.5	8.2	52.5
	2	6	24 (4)	5.5	38.8	8.8	61.2
	3**	2	12 (2)	7.8	32.6	16.7	67.4
	4	6	18 (3)	5.2	35.0	9.6	65.0
	19***	1	18 (4)	9.6	38.8	14.2	61.2
	20	6	18 (4)	6.3	31.4	13.5	68.6
	Total/Mean/%		102 (19)	6.6	37.0	11.0	63.0

during September, October and November, respectively. Fieldwork terminated in November due to extremely dry conditions resulting in males irregularly attending bowers. During S83 we made 90h of direct observation during November, until heavy rains hampered fieldwork. The last 12h observation cycle in November had to be postponed until 5 December, but December data are combined with November results herein. Fieldwork then ceased because continuing torrential rains resulted in males irregularly attending bowers.

To analyse diurnal variation we subdivided the totals for male attendance levels into four periods (0600-0900, 0900-1200, 1200-1500, 1500-1800h). This made data directly comparable with a similar study of Tooth-billed Bowerbirds *Scenopoeetes dentirostris* (see Frith & Frith, 1994). We used the same periods to analyse vocalisation frequencies (see below).

Determining actual time a bower-owning male spent at his bower site was often difficult. Most times we saw an absent male return by flying to one of his favoured perches, or onto his bower perch. However, sometimes the first indication of his renewed presence was when he called. If he remained out of sight but continued to call we assumed he was present, especially if later he flew to another perch, to the bower, or away from his bower site. If we did not re-sight or hear him

we considered his time present to be ended at his last recorded call, even though he may have subsequently remained above the bower for some (limited, in our experience) time. We usually saw the male fly off, but sometimes he would fly unseen higher into the canopy and we were unsure if he had left, unless he gave progressively distant vocalisations as departing. Thus, times presented in Tables 1-3 for males spent at their bower sites are minimums. Having said that, the times we recorded each of the six males at their bower sites were similar each season. This suggests that any discrepancy between the time we recorded present and the actual time involved may be minimal. Single call notes (see below), occasionally heard some distance (>30-40m) from bower sites during a male's apparent absence, were discounted as indicative of his presence, as we could not confirm they were in fact given by the bower owner.

BOWER OWNERSHIP. Males were mist-netted at or near bowers and marked with a metal Australian Bird and Bat Banding Scheme band and a unique two colour band combination (= marked), and released at the capture location. Banded males included not only the owners of the six bowers under intensive observation, but also males intruding from adjacent bowers.

Males attending four of the six bowers in S82 had regularly attended their respective bowers as

TABLE 2. Monthly bower attendance by male Golden Bowerbirds during September, October and November of the display season of 1982.

Months	Bower site number	Hours and (numbers) of observations	Absence		Presence	
			Mean mins per absence	% of total time absent	Mean mins per presence	% of total time present
September	1	12 (2)	13.6	75.3	4.6	24.7
	2	24 (4)	18.6	72.5	7.2	27.5
	3	24 (4)	18.3	67.2	9.6	32.8
	4	24 (4)	15.6	48.8	16.4	51.2
	19	27 (5)	14.7	60.0	9.5	40.0
	20	27 (5)	16.9	57.2	13.6	42.8
Total/Mean/%		138 (24)	16.4	62.0	10.3	38.0
October	1	24 (4)	11.2	62.0	7.0	38.0
	2	24 (4)	11.4	62.6	6.8	37.4
	3	24 (4)	13.4	61.5	8.5	38.5
	4	24 (4)	10.0	54.6	8.5	45.4
	19	27 (5)	10.4	63.1	6.4	36.9
	20	24 (4)	16.1	70.2	7.0	29.8
Total/Mean/%		147 (25)	11.8	62.0	7.3	37.6
November	1	12 (2)	12.7	72.2	5.0	27.8
	2	12 (2)	11.8	65.3	6.4	34.7
	3	12 (2)	18.5	74.4	6.8	25.6
	4	12 (2)	10.5	58.1	7.4	41.9
	19	12 (2)	17.9	72.1	7.2	27.9
	20	12 (2)	21.1	82.2	4.9	17.8
Total/Mean/%		72 (12)	14.8	71.0	6.3	29.0

adult-plumaged individuals since at least S78. In S83 three of them (at bowers 2, 4 and 20) remained in attendance, but the male at bower 19 had been replaced by another male we first caught (at bower 19) in adult plumage in May 1982. The male attending bower 1 in S82 was first caught as an immature in March 1979, when he had just taken the site over and was building a new bower there. He acquired adult-plumaged in S80. The male attending bower 3 was still immature (female-plumaged) during the first season (S82) of this study. We first banded him in March 1979, at a point 140m from bower site 3. He attained adult-plumage during the second season (S83) of this study.

MALE BEHAVIOUR AT BOWERS. Male behaviour at bowers was categorised as: periods of advertisement song, or other calls (including single notes and medleys); bower maintenance; displacement chases; displays; and silence. Advertisement song and other calls were given from favoured perches above or within 15m of the bower, and were timed and totalled separately as they involved no other behaviour. Single calls were too brief (mostly <2secs) to time

meaningfully, and so we estimated their totals by allowing 2secs for each. Calls given during bower maintenance, displacement chases and display periods were, however, included in time periods totalled for those activities. The number, behaviour and vocalisations of female-plumaged and adult male visitors/intruders to bowers were monitored and their presences timed. Numbers of decoration thefts by rival bower-owners were recorded. Numbers, distances from bowers, and heights of habitually-used perches were noted. The length of time favoured perches were used at bower sites 2, 4 and 19 during S82 was recorded.

Bower maintenance periods included time a male was on the bower perch and adding a decoration or a stick to it, or adjusting and/or tidying. Most visits to the bower perch were solely for maintenance, but some were exclusively to display. Sometimes a male displayed on the bower perch before starting maintenance. In the latter case each behaviour was timed separately. Similarly, when a display was instantly followed by a displacement chase both periods of behaviour were treated separately even when directed at the same visitor/intruder.

TABLE 3. Variation in diurnal bower attendance levels of male Golden Bowerbirds during the display seasons of 1982 and 1983.

Season/time	Month	Hours and (number) of observations	Absence		Presence	
			Mean mins per absence	% of total time absent	Mean mins per presence	% of total time present
1982 0600-0900	September	33 (11)	9.8	57.3	7.4	42.7
	October	36 (12)	7.4	51.6	7.0	48.4
	November	18 (6)	9.0	62.3	5.6	37.7
	Total/Mean/%	87 (29)	8.6	56.0	6.8	44.0
0900-1200	September	39 (13)	11.5	49.5	11.7	50.5
	October	39 (13)	12.3	59.3	8.7	40.7
	November	18 (6)	13.8	65.0	7.9	35.0
	Total/Mean/%	96 (32)	12.3	56.4	9.7	43.6
1200-1500	September	33 (11)	24.9	69.2	12.4	30.8
	October	36 (12)	15.5	71.8	6.4	28.2
	November	18 (6)	21.7	82.4	5.1	17.6
	Total/Mean/%	87 (29)	17.2	73.0	7.8	27.0
1500-1800	September	33 (11)	29.1	74.9	10.6	25.1
	October	36 (12)	12.4	67.1	6.4	32.9
	November	18 (6)	16.1	73.1	6.2	26.9
	Total/Mean/%	87 (29)	17.2	71.3	7.3	28.7
1983 0600-0900	November	30 (10)	5.5	34.2	10.4	65.8
0900-1200	November	30 (10)	6.2	37.2	10.2	62.8
1200-1500	November	25 (9)	8.4	44.3	10.6	55.7
1500-1800	November	17 (6)	6.1	31.7	12.5	68.3

Each period of display included one to several display elements. A display element consisted of any one of the three distinct displays performed by male Golden Bowerbirds.

Chi-squared tests and Student's two-tailed *t*-tests were used for statistical comparisons. Percentage data were normalised by applying arcsin transformation. Means are given as \pm one standard deviation. In some instances we also present standard error, to facilitate comparisons with data presented by other bowerbird studies.

RESULTS

ANNUAL SEASONALITY OF BOWER ATTENDANCE BY MALES. Regular seasonal attendance of traditional sites and bowers, by their traditional owners, typically started on the Paluma Range in late August/early September. The commencement, length, and termination, of a display season varied from year to year, primarily in response to climate and/or fruit phenology, as illustrated by results of the first three seasons of our study (August 1978 to February 1981).

We recorded the seasonally first bower advertisement songs during 14-17 August at the start of S78, and by 21 August some bowers had a few decorations on them. By early September most bowers were moderately decorated, with new sticks added to them. From the second week of September until the end of December bower sites were regularly attended by their traditional owners. Rainfall was slightly above average for the time of year (Fig. 1). Temperatures increased during these months, from an average of 19°C in September to 25°C in December, and fruits and insects were plentiful (Fig. 2A, B). Bowers remained moderately decorated and attended until the end of December, but then activities decreased as rainfall increased. During the last week of January, 594mm of rain fell and bower attendance ceased. Rain continued throughout February, to 15 March, as bower decorations deteriorated. No advertisement song was heard, but limited faeces beneath favoured perches indicated some males had briefly visited bower sites (Fig. 2C). During brief dry spells, one or two fresh decorations were sometimes placed on bowers. There was then a brief period of renewed activity during late March to the first week of

May, but bowers were poorly decorated and few advertisement songs given (Fig. 2C).

Bowers were undecorated/unattended during June/July 1979, and not until 19 August did we hear the first advertisement song, marking the commencement of S79. During September 1979, rainfall was average for the month and temperatures rose, but the fruit crop was sparse and remained so throughout the display season (Figs 1, 2A). Insects, including Coleoptera, were less abundant than the previous season (Fig. 2B). October and November were exceptionally dry and hot with rainfall (64mm) well below the seasonal average (230mm). During November, fewer advertisement songs were heard and, while bowers were poorly/moderately decorated, faecal samples indicated males were attending bowers if not maintaining them (Fig. 2C). It remained dry until 25 December; by which time bower attendance had declined, few calls were given, and bower decorations dried and were not replenished. It rained heavily from the last week of December until 12 March, with little or no bower attendance. As in the previous year, there was renewed activity during March, as rains eased, that lasted until about the second week of May.

There was a notable increase in available fruit crop during winter months of 1980 (Fig. 2A). Some bower owners placed a few decorations on traditional bowers by mid-June-July, started advertisement song, and accumulating faeces indicated males were now spending time at bowers (Fig. 2). This winter attendance continued through to August, possibly because of a larger fruit crop. By August 1980 all bowers were regularly attended, despite lack of rain (Fig. 1). Temperatures increased notably in September, insects were abundant, and fruit plentiful; and bowers were well attended as indicated by faeces at them (Fig. 2). Rainfall during September-December was near seasonal average, but from 1 January was excessive, falling every day until 26th (2201mm; see Fig. 1). Bower decorations deteriorated during January and, while no advertisement song was heard, faeces indicated males occasionally visited bower sites (Fig. 2C).

We did not monitor bower activities as closely over the next three years, but seasonal trends showed a similar pattern with regard to relative rainfall. In S81 bower activities commenced during mid-August and lasted until mid-November when, due to heavy rain (468mm), they slowed and then ceased in December (Fig. 1). During

October and November of S82 it was exceptionally dry (71mm), and bower activity levels were similar to those described for S79 (see above). The display season commenced earlier the following season, much as for S80. In S83 rainfall was near the seasonal average, and bower activities persisted until the commencement of the January rains. Bower attendance levels, and behaviours and vocalisations at traditional bowers during S82 and S83, are discussed in detail below.

RELATIVE LEVELS OF BOWER ATTENDANCE BY MALES. *Seasonal variation.* During S82 males spent an average of 36% of total time at their bowers (Table 1), proportional differences between individuals not being significant ($\chi^2 = 4.46$, $P > 0.30$). During S83 males spent an average of 63% of total time at their bowers (Table 1), proportional differences between individuals likewise not being significant ($\chi^2 = 2.72$, $P > 0.70$). Males spent an average of 8 (SE = 0.8) and 11 (SE = 1.3) mins at bowers per presence, and absences averaged 13.9 (SE = 1.7) and 6.6 (SE = 0.7) mins during S82 and S83 respectively. Mean number of visits per hour was 2.7 (range 2.2-3.3) and 3.4 (range 2.6-4.2) during S82 and S83 respectively. Thus, all males attended their bowers for far less (27%) time, less frequently, and for less time per visit, during S82 than during S83 (Table 1).

Monthly variation. During S82 there was a significant difference between the proportion of total time individual males spent at bowers during September ($\chi^2 = 13.74$, $P < 0.02$), because not all started attending bowers at the same time and/or with the same intensity (Table 2). At bower 1, the owner was not sighted on 13 September (the first S82 observation), but two immature males were briefly (<5% of observation) seen adjusting its decorations and sticks. These young males gave occasional *screech* and *scold* notes near the bower, but no advertisement song. No birds were here on 14 September but at our next observation, on the 27th, the traditional owner was regularly attending; but at a mean duration per presence lower than other males (Table 2).

At bower 4, male attendance was notably high in September 1982 (Table 2); apparently because a male new to it, in his first year of adult plumage, was regularly attending (51% of total time) on 9 and 10 September (the first two S82 observations). We assumed he was the new owner, but during our next two observations, of 21 and 22

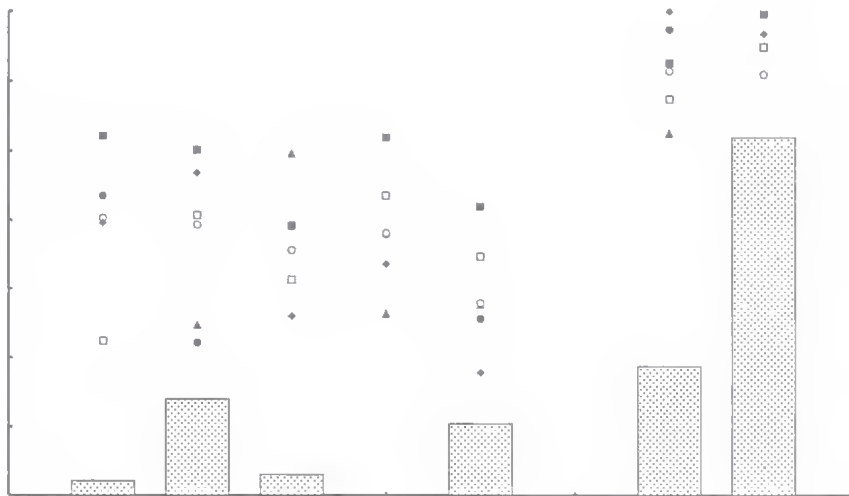


FIG. 3. The percentage of total time that each of six adult male Golden Bowerbirds spent attending their traditional bower site, during bi-weekly periods of the display seasons of 1982 (1 Sept.-15 Nov. 1982) and 1983 (Nov. 1- Dec. 15), relative to the amount of rain (column) that fell during each period. Symbols indicate the bower sites: + = 1, □ = 2, ● = 3, ■ = 4, ○ = 19, u = 20 (see Tables 1 & 2).

September, the traditional owner was in regularly attendance (50% of total time); presumably having displaced the challenger. Mean duration per presence of the challenger (28.9 mins) during the first two September observations was far greater than that of the owner (11.4 mins) during the latter two observations, and was greater than that of other individuals during September or any other month (Table 2). Male attendance at bower 4 remained relatively high throughout S82.

September S82 rainfall was average, but October was exceptionally dry and hot (only 6mm of rain, on the 4th; Fig. 1). Male bower attendance levels increased little during October over those of September, actually decreasing slightly in the middle of the month, with mean duration per presence lower (Table 2, Fig. 3). There was no significant difference between the proportion of total time individual males spent at bowers ($\chi^2 = 3.54$, $P > 0.50$). November rainfall (68mm) was well below the average (157mm), the first two weeks being particularly dry (21mm). By mid-November bowers were poorly maintained and decorated, few advertisement songs were given, and attendance levels decreased considerably (Table 2, Fig. 3). There was a significant difference between time individual males spent at bowers during November ($\chi^2 = 11.55$, $P < 0.05$), because they stopped attending bowers at different times (Table 2). Despite much more

rain in December, attendance levels did not recover, males were rarely sighted at bowers.

In S83 rainfall was near average (Fig 1). Although we made observations only during November 1983, bower attendance by all individuals was much higher (63%) than in September (38%), October (38%) or November (27%) of S82 (Tables 1, 2; Fig. 3). There was no significant difference between the proportion of total time individual males spent at bowers ($\chi^2 = 2.72$, $P > 0.70$) in November of S83.

Diurnal variation. During 0600-0900, 0900-1200, 1200-1500 and 1500-1800h of S82 males spent 44, 44, 27 and 29% of total time attending bowers respectively, differences between these proportions being significant ($\chi^2 = 7.15$, $P < 0.10$). Thus males spent much more S82 time attending bowers in mornings than afternoons, a trend apparent during September, October and November (Table 3).

During the same four diurnal periods of S83 males spent 66, 63, 56 and 68% of total time attending bowers respectively, differences between these not being significant ($\chi^2 = 1.41$, $P > 0.70$). Thus, male attendance levels at bowers were much higher in S83 than in S82, both in mornings (by 21%) and afternoons (by 34%). Mean duration per bower attendance was higher throughout the day in S83 than in S82 (Table 3).

MALE BEHAVIOUR AT BOWERS. *Habitual perches.* Males had several favoured perches

TABLE 4. Time-budgeted activities performed by individual male Golden Bowerbirds at bower sites during the display seasons of 1982 (September, October and November) and 1983 (November). * = immature male during season 82; ** = data for bower 3 excluded; see Results.

Season	Bower site number	Advertisement song			Other calls			Maintenance	
		Mean secs per song	Mean no. rattles per song	% of time present	Single	Medley		Mean secs per period	% of time present
1982	1	38	8	9.1	1.1	105	3.6	61	7.8
	2	39	7	7.1	1.5	121	3.9	70	7.1
	3 *	36	10	5.1	2.0	279	34.5	63	5.8
	4	32	9	5.4	1.0	125	4.3	48	4.9
	19	37	6	6.2	1.0	119	2.9	56	5.3
	20	35	7	6.5	1.0	107	4.8	62	4.7
Total/Mean/%		36	8	6.4	1.2	177 (111**)	8.7 (5.4**)	59	5.8
1983	1	31	9	7.8	0.4	72	2.9	62	3.0
	2	31	9	4.4	0.2	101	4.6	45	3.5
	3 *	33	9	6.8	0.4	110	6.1	20	0.6
	4	34	10	4.9	0.3	63	2.7	43	3.6
	19	28	8	4.6	0.7	143	15.4	37	5.4
	20	27	7	4.2	0.4	106	3.6	22	0.5
Total/Mean/%		30	9	5.1	0.4	110	5.9	40	2.8

Season	Bower site number	Displacement chases		Display		Silence	Total time present (mins)		
		Mean secs per chase	% of time present	Mean secs per display	% of time present	% of time present			
1982	1	34	0.9	59	1.6	75.9	925		
	2	11	0.2	44	1.5	78.7	1185		
	3 *	20	0.4	60	0.9	51.3	1210		
	4	50	1.0	66	1.0	82.4	1693		
	19	20	0.2	64	0.8	83.6	1444		
	20	34	1.1	48	1.0	80.8	1250		
Total/Mean/%		31	0.6	58	1.1	76.2	7707		
1983	1	36	1.1	76	1.3	83.5	378		
	2	39	0.4	35	1.2	85.7	881		
	3 *	43	1.3	60	1.0	83.8	485		
	4	47	1.5	51	1.8	85.2	702		
	19	31	0.6	36	0.8	72.5	665		
	20	21	0.3	35	0.6	90.4	741		
Total/Mean/%		38	0.8	43	1.1	83.9	3852		

above and around their bower, on which they gave advertisement vocalisations, perched silently, or preened. Of a total 947 occasions (S82 and S83 combined) that males were recorded perched above/around the bower, 99.6% involved horizontal branches, mostly of saplings or small trees, and the remainder horizontal to gently sloping vines. Where some of these horizontal branches abutted the plant's vertical trunk (5% of perches used), males sometimes

placed sticks to form small arboreal subsidiary bower structures. During S82 males used an average of 11.7 ± 3.9 perches per observation period ($n = 61$), at a mean of 4.9 ± 2.5 m above ground, and 9.5 ± 2.6 m distant from the bower perch. During S83 these figures were 13.1 ± 4.1 m, 6.3 ± 1.9 m and 9.0 ± 2.6 m ($n = 19$) respectively. During S82 males at bowers 2, 4 and 19 spent 15% of their time perched above their bowers on perches known to be favoured ones.

Advertisement song. This consisted of a prolonged pulsating *rattle* note, typically lasting one or two seconds, that was usually repeated a number of times. It was difficult to precisely locate a bird giving this call, and others. Occasionally males gave only one *rattle*, or a series of one to three, when first arriving back at the bower and before commencing a much longer song (up to 27 *rattles* being recorded). Number of *rattles* per song averaged eight in S82 and nine in S83, each song averaging 36 and 30 secs respectively (Table 4). During some visits males only maintained bowers, and did not give advertisement song, whereas during others they gave several sets of *rattle* song (10 songs being the most during a single visit). Males gave advertisement song on 48% of 1706 bower visits in S82, and on 61% of 645 visits in S83.

Males spent 6.4 and 5.1% of time present at bowers giving advertisement song during S82 and S83 respectively (Table 4). There was no significant difference between the proportion of time individual males spent giving advertisement song at their bowers each season (82: $\chi^2 = 1.57$, $P > 0.90$; 83: $\chi^2 = 2.02$, $P > 0.80$), nor were differences between them for the two seasons significant (arcsin transformation $t_{10} = 1.39$, $P > 0.20$). Mean duration of each song period was similar during each month of S82 (Tables 5 & 6).

During September of S82, as males re-established themselves, individuals spent more time at bowers giving advertisement song (7.5%) than in October (5.9%) and November (5.0%). Mean duration of each song was also longer (Table 5). The male at bower 1 did not start bower attendance until late September, but was particularly vociferous (Table 5). The lower S82 October and November figures may have reflected extremely dry conditions; but in S83, when climate was more favourable, males still spent only 5.1% of their presence giving advertisement song (Table 4; Figs 1,2).

Males spent more of their presence at bowers giving advertisement song during mornings than afternoons during S82 and S83 (Table 6); proportional differences between diurnal periods (data for both seasons combined) being significant (arcsin transformation, $t_4 = 5.33$, $P < 0.01$). Mean duration of songs was similar at different times of day (Table 6). In S82 males performed 37, 43, 11 and 9% of songs ($n = 819$) during 0600-0900, 0900-1200, 1200-1500 and 1500-1800h respectively. In S83 they performed 46, 27, 14 and 13% of songs ($n = 391$) during the same periods respectively.

Other calls. These consisted of single calls or a continuous medley of them. Single ones were a *squeal*, *screech*, *scold-rasp*, or *wolf whistle* as follows: *squeal* was a high-pitched thin and variable note; *screech* a variable, harsher and lower, but louder and more assertive, note sometimes delivered with a rather braying-like quality; *scold-rasp* a loud and urgent note(s); and *wolf-whistle* a powerful, two note, harsh and dry, *squeal/screech* notes with the same cadence and timing as a human 'wolf-whistle'.

Single calls, such as *screech* and *wolf-whistle*, were mostly given as males approached or left their bower site, or when conspecifics were close. They were also heard some distance away from bowers, while owners were absent and presumably foraging. The *scold-rasp* was sometimes given when an inter-specific bird, larger than the bower-owner, such as a Spotted Catbird, *Ailuroedus melanotis*, or Satin Bowerbird, *Ptilonorhynchus violaceus*, came close to or onto the bower. Once when an Australian Brush-turkey, *Alectura lathami*, walked over a bower the male owner scolded it for 60secs, until it left.

During S82 and S83 males gave single calls for 1.2% and 0.4% of time present at bowers, respectively (Table 4). The proportion of single calls given was broadly similar each month of S82 (Table 5), and for different times of the day (Table 6), during both seasons.

A medley included a continuous series of single calls interspersed with frog- and cicada-like notes, a single *rattle* with a *squeal(s)* and/or vocal avian mimicry. At least 22 bird species were identified as models for mimicry performed: White-headed Pigeon, *Columba leucomela*; Red-tailed Black Cockatoo, *Calyptorhynchus banksii*; Sulphur-crested Cockatoo, *Cacatua galerita*; Australian King-Parrot, *Alisterus scapularis*; Crimson Rosella, *Platycercus elegans*; a cuckoo; Noisy Pitta, *Pitta versicolor*; Yellow-throated Scrub Wren, *Sericornis citreogularis*; Large-billed Scrubwren, *S. magnirostris*; Brown Gerygone, *Gerygone mouki*; Mountain Thornbill, *Acanthiza pusilla*; Bridled Honeyeater, *Lichenostomus frenatus*; Grey-headed Robin, *Heteromyias albispecularis*; Chowchilla, *Orthonyx spaldingii*; Eastern Whipbird, *Psophodes olivaceus*; Bower's Shrike Thrush, *Colluricincla boweri*; Barred Cuckoo-shrike, *Coracina lineata*; Pied Currawong, *Strepera graculina*; Victoria's Riflebird, *Ptiloris victoriae*; Spotted Catbird; Tooth-billed Bowerbird; Satin Bowerbird and many small passerine notes we did not identify.

TABLE 5. Monthly time-budgeted activities performed by individual male Golden Bowerbirds at bower sites during September, October and November of the display season of 1982. * = immature male during season 82; ** = % of time present with data for bower 3 excluded; see Results.

Months	Bower site number	Advertisement song		Other calls			Maintenance	
		Mean secs per song	% of time present	Single	Medley		Mean secs per period	% of time present
September	4	46	16.2	1.7	58	2.2	77	19
	2	53	8.7	1.7	150	7.0	71	7.8
	3*	77	0.5	3.1	439	38.8	46	2.6
	4	31	7.0	7.3	197	7.3	50	2.5
	19	46	3.1	7.8	195	3.5	77	3.2
	20	34	7.5	0.9	69	3.1	69	3.3
Total/mean/%		46	2	3.1	237 (140**)	9.7 (5.8**)	54	4
October	1	46	3.4	1.2	69	3.3	66	4.7
	1.6	33	6.7	1.6	77	3.1	71	7.3
	3*	46	5.4	2.9	227	30.0	3.4	8.5
	4	35	4.7	1.2	77	2.9	53	7.3
	19	33	5.4	1.6	69	1.6	67	7.0
	20	46	7.0	1.6	138	7.0	52	5.1
Total/mean/%		46	5.6	1.6	144 (87**)	7.9 (5.0**)	7.3	7.0
November	1	31	4.8	1.1	139	7.3	80	7.3
	4	31	5.6	0.9	142	2.8	69	5.6
	3*	28	5.2	1.1	195	37.1	53	0.9
	4	36	5.5	7.3	79	2.9	34	7.3
	19	31	2.5	8.5	121	0.9	1.7	0.9
	3.1	36	7.0	7.3	69	0.7	87	11.3
Total/mean/%		31	0.2	0.8	154 (112**)	8.5 (5.4**)	56	0.3

Months	Bower site number	Displacement chases		Display		Silence	Total time present	
		Mean secs per chase	% of time present	Mean secs per display	% of time present	% of time present		
September	4	33	1.6	23	3.1	70.2	178	
	2	0	4	46	0.9	74.2	396	
	1.6	22	0.3	33	1.1	52.2	472	
	4	69	0.9	53	3.4	83.5	1.7	
	19	7.0	0.2	62	0.9	76.7	646	
	20	31	0.9	46	7.0	83.8	693	
Total/mean/%		31	0.9	33	7.3	76.8	3122	
October	4	33	1.1	53	1.3	76.9	547	
	2	0	0.2	53	1.3	80.6	539	
	31	2.9	7.0	75	1.6	51.2	554	
	4	77	1.6	61	0.9	80.6	656	
	19	33	0.2	58	1	82.6	597	
	20	32	0.7	33	8.5	76.7	429	
Total/mean/%		46	0.7	58	1.2	75.3	3320	
November	4	29	0.7	71	7.0	73	200	
	2	19	7.3	53	0.7	81.7	200	
	3*	0	0.9	31	1.6	79	184	
	4	31	0.5	79	2.9	82.5	302	
	19	19	0.3	34	1.3	86.3	201	
	20	39	4.0	0	0	73.7	128	
Total/mean/%		28	0.8	67	2.4	76.4	1265	

Golden Bowerbirds mimicked more than one call of a given bird species. For example, both the whistle call and alarm flock note of Crimson Rosellas, the whistled single note and the 'cheep-cheep' greeting calls of Grey-headed Robins, the whip-crack song and the 'chip-chop' calls of Eastern Whipbirds, the single 'tick' note, 'e-i-or' and 'any-higher' calls of Spotted Catbirds, and both 'chuck' and coarse rattling flight alarm calls of Tooth-billed Bowerbirds. We once witnessed mimicry of the flight wing-noise of adult male Victoria's Riflebirds.

Mimicry was sometimes opportunistic; that is to say in immediate response to the call or sighting of a model bird species. For example, a male Golden Bowerbird returned to his bower to find a Spotted Catbird perched three meters from it and then immediately mimicked a catbird call, even though the visitor was silent. Neighbouring Golden Bowerbirds often instantaneously respond to each others vocalisations, as between males at bowers 19 and 20 located 130m apart. When one male gave a song of *rattles* the neighbour would immediately do likewise.

During S82 and S83 males gave medleys for 8.7 and 5.9% of their time present at bowers, these vocalisations averaging 177 and 106secs, respectively (Table 4). The higher percentage of medleys in S82 was primarily due to the vocal efforts of the immature male at bower 3, in his first season of regular attendance. During S82 he spent 35% of his bower presence giving medleys, averaging 278secs in duration (Table 4). This percentage was high every month of S82 (Table 5). This immature gave some medleys from the bower perch, unlike adult males, (for a total of 8mins). Adult males gave medleys for an average of only 5.4% of time, at an average of 111sec duration, from favoured perches. By excluding bower 3 data, results for S82 were similar to those of S83 (see Tables 4-6). The male at bower 3 was in adult plumage in S83 and during this, his second year of regular bower attendance, gave fewer medley calls (Table 4). The new (but adult-plumaged) male at bower 19 in S83 gave a greater proportion of medleys, and for longer periods, than other males during that season (see Table 4).

During S82 males gave more afternoon medleys than morning ones, a trend reflected not just by the male at bower 3 (see above) but by other individuals (Table 6). During S83 such diurnal variation was not apparent, and males spent more of their time giving medleys during both

0600-1200 and 1200-1800h than during these periods in S82.

Of 228 and 125 medley calling periods in S82 and S83, we confirmed a conspecific (usually female-plumaged) was near/at the bower on 14% and 29% of occasions, respectively. Medley calls were sometimes given before/after displacement chases or displays (see Table 7).

Bower maintenance. Bower maintenance involved a male placing a newly collected decoration/stick on the bower, flying down to the ground below the bower perch to retrieve a fallen decoration, or flying up onto a tower to adjust/move a stick. It also included brief visits to the bower to inspect and/or to remove a leaf from the structure. Sometimes the owner flew to a nearby vertical sapling (<1m from the bower) specifically to be able to inspect his newly adjusted bower decorations/sticks; before returning to continue bower maintenance, flying off to a favoured perch, or flying directly out of the bower site.

Males flying to their bower to maintain it were usually silent (77% of 615 such visits in S82 and S83), but during 140 other visits males called briefly as they landed on their bower perch. Such calls included: a single *rattle* with one or two *squeal(s)* ($n=101$), a single *rattle* with *squeals* followed by brief mimicry or *screeches* ($n=10$), a single *rattle* with a *cicada* or *screech* call ($n=9$), or just one *rattle*, *squeal*, mimicry or *screech* ($n=20$). Most such calls (94%) occurred when males were not carrying anything. Males remained silent once decorating/maintaining bowers.

Males returning to their bower site with a decoration or stick usually went directly to the bower, to add it to the structure. Most decorations (95%) were collected by males during their absence from the bower, having harvested them or stolen them from a neighbouring bower. A few times (5%) males did not leave the bower area to collect a decoration, but merely flew to a tree (often out of our sight) to return within <30secs with a decoration. On four such occasions we confirmed the male had gone to a 'store' to retrieve a decoration. We also twice saw a male fly from his bower with a decoration to 'store' it in a tree crevice. Three times we saw a male take a decoration from his bower to place it on a favoured perch, only to subsequently collect it and return it to his bower. Unlike bower decorations, most sticks (77%) were collected near (10-20m distant) the bower. Sticks (to 30cm long) were usually collected one at a time, but a couple

TABLE 6. Variation in diurnal time-budgeted activities performed by individual male Golden Bowerbirds at bower sites during the display seasons of 1982 and 1983. * = data for bower 3 excluded; see Results.

Season/time	Month	Advertisement song		Other calls			Maintenance	
		Mean secs per song	% of time present	Single % of time present	Medley Mean secs per call	% of time present	Mean secs per period	% of time present
1982 0600-1200	September	40	10.2	0.9	129	4.9 (3.3*)	57	5.4
	October	38	7.5	1.4	106	5.0 (1.5*)	69	8.8
	November	32	6.9	0.5	171	6.2 (2.1*)	56	5.8
	Total/mean/%	38	8.5	1.1	124	5.2 (2.4*)	62	6.8
1200-1800	September	30	2.5	1.4	398	18.6 (5.0*)	42	1.3
	October	30	3.4	1.8	185	12.1 (4.8*)	51	5.2
	November	28	2	1.3	142	12.3 (4.8*)	57	6.5
	Total/mean/%	30	2.8	1.6	236	14.6 (4.9*)	51	4.0
1983 0600-1200	November	30	6.2	0.3	114	6.1	41	2.6
1200-1800	November	30	3.4	0.5	104	5.7	37	3.3

Season/time	Month	Displacement chases		Display		Silence	Total time present (mins)	
		Mean secs per chase	% of time present	Mean secs per display	% of time present	% of time present		
1982 0600-1200	September	39	0.7	48	0.6	77.3	2016	
	October	32	0.8	61	1.3	75.2	1999	
	November	37	0.6	62	2.1	77.9	785	
	Total/mean/%	35	0.7	58	1.1	76.6	4800	
1200-1800	September	13	0.1	31	0.3	75.8	1106	
	October	26	0.7	53	1.1	75.7	1321	
	November	24	1	73	2.8	74.1	480	
	Total/mean/%	25	0.5	56	1.1	75.4	2907	
1983 0600-1200	November	40	1.0	45	1.2	82.6	2316	
1200-1800	November	32	0.5	41	1.0	85.6	1536	

of times two or three sticks fused together were carried in. Most sticks were taken from the ground, but three times a male broke a dead stick off a sapling.

During S82 males visited bowers 451 times to maintain them, adding a new decoration on 222 (49%) occasions, and a stick on 47; remaining visits involving only maintenance. Of 222 decorations, 56% were beard lichen (*Usnea* sp.), 32% the creamy-white persistent flowers, or seed pods of Melicope (*Melicope broadbentiana*), 3% jasmine (*Jasminium kajewskii*) or orchid (*Dendrobium* sp.) flowers, and 9% unidentified. During S83 males visited their bowers 168 times to maintain them; adding a new decoration on 64 (38%), and a stick on five, occasions. Remaining visits involved only maintenance. Of 64 decorations, 36% were beard lichen, 20% Melicope, 22% jasmine or Brown Silky Oak (*Darlingia*

darlingiana) flowers, and 22% unseen or unidentified.

Males spent more time in bower maintenance during S82 (5.8%) than during S83 (2.8%), and for longer durations per period (Table 4). There was no significant difference between the proportion of time various individual males spent maintaining their bowers each season (82: $\chi^2 = 1.33$, $P > 0.90$; 83: $\chi^2 = 6.5$, $P > 0.20$), but differences between them for the two seasons were significant (arcsin transformation $t_{10} = 6.92$, $P < 0.001$). In September S82 most individuals spent less time maintaining bowers, particularly in the afternoon, than during October and November (Tables 5, 6).

In S82 males performed 48, 22, 13 and 17% of total maintenance visits ($n = 451$) during 0600-0900, 0900-1200, 1200-1500 and 1500-1800h, respectively. Most decorations (70% of

222) and sticks (72% of 47) were collected during the morning (0600-1200h). In S83 males performed 24, 29, 30 and 17% of total maintenance visits ($n = 164$) during the same periods, respectively. Most decorations (67% of 64) were added in the morning (0600-1200h). Of the five S83 stick collections (see above), two were in the morning and three the afternoon.

Displacement chases. When a conspecific or other bird landed on the bower perch, or one near it, bower-owners usually responded by flying at, and displacing, the visitor to chase it out of the bower site. While chasing, the bower-owner often fanned his tail and, when landing on the bower perch to displace the visitor, gave a single rattle with *squeal(s)*. During the ensuing chase, calls also included a single rattle followed by *cicada* and/or other brief mimicry.

Of 95 displacement chases observed during S82, 80 were directed at conspecifics, 11 at other birds, and recipients of four were unseen. Of 49 displacement chases seen during S83, 29 were directed at conspecifics, nine at other birds, and recipients of 11 were unseen. Thus, of 144 displacement chases, 76% were directed at conspecifics and 24% at other birds. Other species included: White-throated Tree-creeper, *Cormobates leucophaeus* ($n = 1$); Bridled Honeyeater ($n = 1$); Yellow-throated Scrub-wren ($n = 2$); Grey-headed Robin ($n = 10$); Eastern Whipbird ($n = 2$); Bower's Shrike-thrush ($n = 1$); and small unidentified passerines ($n = 3$). Ten of these chases involved displacement from the bower perch and the others (e.g. Yellow-throated Scrub-wren, Eastern Whipbird, Grey-headed Robin) from within 5m of it. An Australian Brush-turkey ($n = 1$), Spotted Catbird ($n = 2$) and Satin Bowerbird ($n = 4$) perching close to and/or on the bower were not chased, but were scolded.

During S82 and S83 conspecifics were seen visiting bowers on 136 and 46 occasions, respectively. Of these 182 visitations: 103 were by female-plumaged (unmarked/sex unknown) individuals; 25 by non-bower-owning immature (female-plumaged) males (identified by bands and/or behaviour); and 54 by neighbouring (marked) bower-owners (Table 7). We usually saw only one visitor at a time, on or near a bower perch, but four times we confirmed a second visitor simultaneously in the bower area.

Female-plumaged individuals (gender unknown) were furtive as they approached a bower, usually via several perches. When they reached the bower perch they adopted a 'sleeked'

and/or 'frozen' posture and peered about, without calling or touching decorations. During 99 of 103 visits by female-plumaged visitors, the bower-owner was present at the bower site (Table 7). On 80 of these 99 visits the owner typically instantly displaced and chased off the visitor, mostly (81%) from the bower perch. After being chased away, some individuals ($n = 8$) immediately circled back to the bower perch, only to be chased off again by the owner. Consecutive displacement of the same visiting individual from a bower perch involved 2 ($n = 6$), 3 ($n = 1$) or 4 ($n = 1$) chases. Owners briefly displayed to some (18%) female-plumaged birds when they first arrived, but once the visitor reached the bower perch it was displaced and chased away. After some chases (8%) owners returned to their bower, sometimes accompanied by the same visitor, to then display (Table 7). On 19 of the 99 visits by female-plumaged birds they were not chased away; the owner displaying to ($n = 6$), or ignoring them as they perched above ($n = 8$) or on ($n = 5$) the bower perch. These visitors may have been female.

Non bower-owning immature males were seen to visit bower sites five times in the owner's absence and 20 times in the owner's presence, these visits averaging 38secs (Table 7). During an owner's absence young males spent more time (mean visit duration = 104secs) on the bower, adjusting decorations and/or sticks, than when an owner was present (mean visit duration = 24 secs). On 18 visits in the owner's presence young males were typically instantly displaced and chased off by the owner, and always so from the bower perch, sometimes giving one or two *squeal/screech* calls as they were chased. Some individuals ($n = 4$) immediately circled back to the bower perch after the chase, only to be chased again. Consecutive chases directed at the same individual involved 2 ($n = 2$), 4 ($n = 1$) and 6 ($n = 1$) chases. Twice an owner displayed and/or gave medley calls when a young male first arrived near his bower, but when the visitor reached the bower perch it was displaced and chased. After two such chases the owner returned to the bower to display briefly (Table 7). On two visits in one owner's presence, young males were not chased away, but this was because the male-owner of bower 3 was immature. He tolerated another young male on his bower for 100 and 159secs (see also below).

Male bower owners visited adjacent males' bowers 54 times, 35 being in an owner's absence and 19 in an owner's presence. On 11 of the latter visits the intruder was chased off the bower perch

TABLE 7. Conspecific visits to six Golden Bowerbird bower sites (data for S82 and S83 combined) and the bower owners reaction to them when in attendance.

Visiting conspecifics		Female-plumaged: sex unknown	Non-bower-owning young males	Bower-owning males	Total/Mean/%	
Visits to bower sites	No. to bower perch	76	22	50	148	
	No. to other perches(<5m distant)	27	4	5	35	
	Total number of visits	103	25	54	182	
	Mean time per visit (secs)	52	38	17	36	
	Bower-owner absent (No.)	4	5	35	44	
	Bower-owner present (No.)	99	20	19	138	
Reaction of bower owners to visitors	Displacement chases	No. from bower perch	64	18	10	92
		No. from other perches (<5m distant)	15	0	1	16
		Total number	80	18	11	109
		% of times owner present	81	90	58	79
	Displays	No. before a chase	14	2	1	17
		No. after a chase	6	2	0	8
		No. without a chase	6	0	0	6
		Total number	26	4	1	31
	Medley calls	No. before a chase	6	1	0	7
		No. after a chase	19	1	1	21
		No. before a display	6	0	0	6
		No. after a display	21	0	0	21
		No. with no chase or display	10	2	1	13

by the owner, but 4 times successfully stealing a decoration. Displacement chases twice involved body contact between adult males. One owner rapidly displaced a rival from his bower perch to grapple with him, the two tumbling toward the ground before separating. The marauder then flew off, pursued by the owner. On 8 of the 19 intrusions there was no chasing; twice the intruder flying off at the owner's return before it could steal. On 6 occasions a thief stole unmolested in the presence of the immature male owner of bower 3.

Thieves managed to steal a decoration during 83% of their visits to bowers of rival males, obviously being most successful (100%) in the owner's absence. Time spent at a rival's bower was brief (mean = 17secs). Decoration theft between adjacent bower-owners was rife. Having apparently noted a neighbouring rival male's absence, by lack of his calls, bower-owners often flew immediately in the direction of the presumably unattended bower to then immediately return with a decoration. For example, when the male at bower 19 was absent (DWF observing there), his immediate neighbour at bower 20 (CBF simultaneously observing there) would fly

to bower 19 and immediately return to his own bower with a stolen decoration.

During our second (14 September) S82 observation, the immature owner of bower 3 was challenged for the site by a male in his first year of adult plumage. Both birds were present at the site for 211 of the 360min observation. Some of this time they perched close to each other, the immature owner continuously giving medley calls with mimicry, frog-like notes and scolds (for 139mins); and the adult-plumaged challenger frog-like notes, scolds and sometimes mimicry. At other times they chased each other in prolonged tail-fanning flights about the bower, or in short flights from perch to perch while fluttering/flicking wings in agitated manner. The adult was mostly chased by the immature, but sometimes this was reversed, the immature twice displacing the adult from a perch but four times the reverse. The adult once performed *Bow* and *Head nod and shake* displays. The immature retained his site, however, and attained adult plumage the following season.

Males spent little (<1%) time present at bower sites in performing displacement chases (Tables 4-6). Displacement chases averaged 34 secs, but varied much between individuals.

Displays. Males performed three basic display elements (*Bow*, *Head nod and shake*, and *Flight/hover*) at bower sites. In the *Bow* the male lowered his bill and head rigidly downwards and erected his crown and nape feathering, thus emphasising his brilliant yellow 'crest', while his wings were slightly to fully drooped (depending on display intensity) and occasionally flicked. The tail was pulled forward beneath the lowered head, and sometimes held to one side.

The *Head nod and shake* involved the male nodding his rigidly downward-pointing bill and head up and down with erect head plumage and, when displaying intensely, also shaking his head from side to side. As he nodded he peered intently at, and sometimes pecked, his perch (usually a vertical sapling trunk). This display also emphasised the yellow central crown and nape 'crest'. The wings were slightly to fully drooped and occasionally fluttered. *Bow* and *Head nod and shake*, or vice versa, may be performed consecutively on the same perch when displaying is intense.

In *Flight/hover* display a male flew with slow and deliberate 'butterfly-like' beats of extensively-opened wings around his bower at 0.5–4 m (usually 1–2 m) above ground, occasionally with a decoration in his bill. During this display flight the tail may be fully fanned during brief mid-flight hovers; thus exposing the yellow outer rectrices. Also in this display, males typically stopped to hover in front of a vertical sapling trunk or its leaves, with bill tip touching the stem/leaves, while repeatedly and alternately fully fanning and closing the tail. The bird then flew 'butterfly-like' to another sapling to perform the hover/tail fanning display again. During *Flight/hover* the male may briefly perch on a vertical sapling stem where he may also perform a *Head nod and shake* display.

Each display consisted of one, two, or all the above three elements. An element was often repeated during a display. During S82 and S83 we recorded a total of 146 displays, involving 238 separate elements: 62 *Bows*, 104 *Head nod and shakes* and 72 *Flight/hovers* (Table 8). Of the 62 *Bow* elements: 48% were performed on bower perches, 44% on vertical sapling trunks and 8% on horizontal perches. The *Bow* was performed alone (24%) or, during other displays, was performed before (23%) or after (29%) *Head nod and shake*, or before (11%) or after (13%) a *Flight/hover* (see Table 8).

Of a total of 104 *Head nod and shakes*: 13% were performed on bower perches; 75% on

vertical sapling trunks; and 12% on horizontal perches (Table 8). Most (90%) times a male performed the *Head nod and shake* on one perch only, but a few times flew to one ($n = 5$) or two ($n = 5$) additional perches in continuous display. The *Head nod and shake* was performed alone (38%) or, during other displays, was performed before (17%) or after (14%) *Bow*, or before (14%) or after (17%) *Flight/hover* (see Table 8).

Of a total of 72 *Flight/hover* displays: 96% were performed at vertical sapling trunks or leaves and the remainder at decorated bower platforms, prior to landing on the bower perch. The number of hovers given during a *Flight/hover* display varied. Most times ($n = 52$) a male performed only one hover; but at other times performed 2 ($n = 9$), 3 ($n = 5$), 4 ($n = 1$) or 5 ($n = 1$). Four flight displays lacked a hover. *Flight/hover* was performed alone (33%) or, during other displays, was performed before (11%) or after (10%) *Bow*, or before (25%) or after (21%) *Head nod and shake* (see Table 8). We could discern no clear sequence in which the three display elements might typically be performed, possibly because no complete successful courtship, to copulation, was observed.

When males landed on their bower perch to display (*Bow* or *Head nod and shake*) they sometimes gave one rattle and squeal, but on other perches gave only a squeal(s). During *Flight/Hover* displays males often gave a squeal(s) and/or brief mimicry, as flying from one perch to another (Table 8). During *Bow* and *Head nod and shake* displays given on bower and other perches, males occasionally (9%) held a decoration in the bill, but only twice when a female-plumaged individual was known to be in the area. Points of saplings used during displays averaged 2.1 ± 1.3 m above ground, and were 3.2 ± 1.8 m ($n = 36$) from bowers.

Total numbers of elements performed during each display (including repetition of any elements; see above) are summarised in Table 9. Most displays involved one (63%), two (23%) or three (16%) elements; but five displays consisted of four, six ($n = 3$) and nine. Of the 238 elements observed: 18 (1.4 per display) were performed exclusively on bower perches, 137 (1.4 per display) on/at vertical perches, 13 (1.1 per display) on horizontal perches and 70 (3.0 per display) on a combination of perch types (Table 9). There was no apparent sequence to display elements. Of total displaying time only 12% was on the bower perch.

TABLE 8. Number and sequence of display elements ($n = 238$) performed by male Golden Bowerbirds at their bower sites during 146 displays, and the number of times males called and carried a decoration in their bill during display (data for display seasons of 1982 and 1983 combined). * = hovers performed in front of vertical trunk or its leaves; ** = hovers directed at the bower tower before landing on the bower perch; see Results.

Display elements			Bow	Head nod and shake	Flight/hover	Total number of display elements	% of total number
Display elements	Number given on/directed at *	bower perch	30	13	3 **	46	19.3
		vertical support	27	79	69	175	73.6
		horizontal perch	5	12	0	17	7.1
		Total number	62	104	72	238	
	Number of single elements only		15	39	24	78	32.8
	Number given with other elements	before a bow	-	18	8	26	10.9
		before a nod& shake	14	-	18	32	13.5
		before a flight/ hover	7	15	-	22	9.2
		after a bow	-	14	7	21	8.8
		after a nod& shake	18	-	15	33	13.9
		after a flight/ hover	7	15	-	26	10.9
		Total number	62	104	72	238	
Calls	No. given on bower perch		12	8	0	20	8.4
	No. given on other perches		4	13	14	31	13.0
Decoration held in bill	No. held on bower perch		10	4	0	13	5.5
	No. held on other perches		3	6	0	9	3.8

Numbers of elements during a display did not increase as S82 progressed, possibly because it was extremely dry. During September, October and November 56, 46 and 61% of displays involved one element, 33, 29 and 26% two, and 11, 11 and 18% three elements respectively. Two six-element displays occurred in late October, and one four-, one six- and one nine-element display in November of S82. During November of S83, display involved one (79%), two (19%) or three (2%) elements.

Of the total 146 displays by bower-owning males we saw a female-plumaged individual simultaneously at the bower site 26 times (22 on the bower perch and 4 perched close by; see Table 7). On these 26 occasions males displayed before/after a displacement chase ($n = 20$) or displayed only ($n = 6$); performing one display element ($n = 17$: five *Bows*, five *Head nods and shakes*, and seven *Flight/hovers*), or two ($n = 5$), three ($n = 3$) or nine ($n = 1$) elements.

The longest display observed (17mins) involved performing display elements nine and three times, each group of them interspersed with much medley calling. A female-plumaged individual was perched on a vertical sapling initially, but then moved to the lower side of a bower tower to perch motionless, with sleeked plumage, and stare at the male. Once, when the visitor landed on the bower perch, it was

immediately displaced and chased by the owner. As in all other display/calling sequences with a female-plumaged individual present, this did not terminate in copulation.

Males spent little (1.1%) time displaying during S82 or S83 (Table 4). During S82 fewer and briefer displays were recorded in September, during both mornings and afternoons, than in November despite decreasing bower attendance during the latter (Tables 5, 6). Mean display duration was 67 secs (Tables 4-6).

Silence and other behaviour: Males spend much time silently on perches above their bower, when they preen, bill-wipe, sun, change perches, turn 180° to face the opposite direction to sing or to better listen to neighbours' calls, or forage locally. When males returned from an absence, having obviously bathed, they flicked their wings, shook and fluffed their damp feathers and continuously preened. Once during a brief rain shower a male shook his wings and fluffed his plumage, before bathing by flying into sapling foliage and briefly fluttering/hovering amongst the wet leaves. On two occasions (at 0942 and 1245) different males perched in direct sunlight above the bower and sunned themselves; with erected breast, rump, head and nape feathers, down-pressed tail and drooped wings. We witnessed males fly from a favoured perch ($n = 28$) to snatch an insect from nearby foliage or

trunk, or to hawk ($n = 2$) an insect from the air. Males were twice seen to fly to take a vine fruit, twice to feed on a fruit on the ground and twice to retrieve fruit from a food store near the bower (a crevice in a vertical trunk).

The proportion of time at a bower that males spent silently (other than during bower maintenance periods, displays or chases) averaged 76% during S82 and 84% during S83 (Table 4). The lower S82 figure was in part due to the continuous medley calls given by the male establishing himself at bower 3. Periods of silence were similar for each individual for each month (Table 5), and during different times of the day during S82 (Table 6).

DISCUSSION

ANNUAL SEASONALITY AND RELATIVE LEVELS OF BOWER ATTENDANCE BY MALES. Paluma Range male Golden Bowerbirds typically started attending traditional bowers in late August/early September, as temperatures initially rise from mid winter ones, approximately 6 to 8 weeks before females commenced egg-laying (Frith & Frith, 1998). On the Atherton Tableland, especially at slightly lower and thus warmer altitudes, the display season starts a few weeks earlier (Marshall, 1954; Frith & Frith, unpubl. data). Bower attendance declined in December; particularly when pre-wet season rains commenced (Warham, 1962; Frith & Frith, 2000b and this study). During the wet season proper, few advertisement songs were heard, decorations deteriorated, and few males briefly visited bowers to add decoration during dry spells. Males moult at this time (Frith & Frith, unpubl. data). A brief period of activity occurred in late March-early May, when bowers were poorly decorated and few songs given, as noted by Warham (1962) on the Atherton Tableland. This post-courtship activity is in part reflected by infrequent attendance of traditional bowers by immature males, a situation also found in Tooth-billed Bowerbirds at the same location (Frith & Frith, 1994; 2000b).

Seasonal variation in time invested at/on bowers by male Golden Bowerbirds may vary year to year subject to prevailing weather conditions, particularly excessive wet season rains and drought, and thus food resource availability (see Lenz, 1993; Frith & Frith, 1994; and this study). During abnormally dry seasonal conditions (as in S79 and S82 of this study), when rainforest fruit crop was poor and invertebrate numbers and biomass low, not only was the

display season shorter and male attendance at bowers reduced, but fewer females attempted to nest or did so successfully (Frith & Frith, 1998). A similar situation was recorded for Paluma Range Tooth-billed Bowerbirds during the dry S79 (Frith & Frith, 1994; 2000b). During seasonally typical conditions, male Golden Bowerbirds attended their bowers at consistent levels throughout the day, as did Macgregor's Bowerbirds *Amblyornis macgregoriae* (see Pruett-Jones & Pruett-Jones, 1982), but in adversely dry conditions they did so almost twice as much during the mornings than during afternoons. Drought conditions had similar impacts upon both sexes of a polygynous, lekking, neotropical hummingbird (Stiles 1992).

Adult male Golden Bowerbirds ($n = 7$) spent an average of 50% (range 32-69%) of daylight within 15-20m of their bowers, at a mean of 2.9 (range 2.2-4.2) bower visits per hour and each averaging 9.5mins in duration. The former figures are similar to those found for male Macgregor's Bowerbirds ($n = 5$) that spent an average of 54% (range 20-75%) of daylight within 15-20m of their bowers, but did so at a mean of 1.4 bower visits per hour (range 0.6-2.0) and each averaging 4.6mins in duration (Pruett-Jones & Pruett-Jones, 1982). Both species are predominantly frugivorous (Pruett-Jones & Pruett-Jones, 1985; Frith & Frith, unpubl. data). Male Tooth-billed Bowerbirds, almost exclusively frugivorous during their peak courtship and mating season, spent an average of 64% of daytime at or near (<10 m) their courts, at a mean of 2.9 court visits per hour and each visit averaging 23mins in duration (Frith & Frith, 1994). Male rainforest Satin Bowerbirds, with a 67% fruit component of annual diet, spent an average of 73% of daytime within 50m of bowers (Donaghey, 1981). A male Great Bowerbird, *Chlamydera nuchalis*, a species considered predominantly frugivorous (Diamond, 1986a; Schodde & Tidemann, 1988), but probably less so than the above species, spent 47% of daylight hours at or near his bower at peak mating season (Veselovsky, 1978).

Regent Bowerbird, *Sericulus chrysocephalus*, annual diet includes 81% fruit, and yet males spent a mere 3% of daytime at or near their bowers at an average of 0.43 bower visits per hour, and each visit averaging 6.7mins in duration (Lenz, 1994). Similarly, a Flame Bowerbird, *S. aureus*, spent 6% of daytime at/near its bower (Dwyer & Minnegal in Coates, 1990) and a Fire-maned Bowerbird, *S. bakeri*,

TABLE 9. The number of display elements ($n = 238$) performed by male Golden Bowerbirds during 146 displays on the bower perch and elsewhere in the bower site (data for the display seasons of 1982 and 1983 combined). * = these include bower perches, horizontal perches and vertical sapling trunks that Bow and Head nod and shake display elements were performed on, and vertical tree trunks or its leaves that the Flight/hover display were directed at; ** = during a display any element may be performed more than once; see Results.

		Number of display elements per display **						Total no. of displays (% of total)	Total no. of display elements (% of total)
		one	two	three	four	six	nine		
Location *	Bower	12	0	0	0	0	0	13 (8.9)	18 (7.6)
	Vertical	68	21	0	0	0	0	99 (67.8)	138 (58.0)
	Horizontal	10	0	0	0	0	0	11 (7.5)	12 (5.0)
	Bower to vertical	0	7	0	0	0	0	8 (5.5)	17 (7.1)
	Bower to vertical to bower	0	1	0	0	1	0	3 (2.1)	11 (4.6)
	Vertical to bower	0	2	0	0	0	0	3 (2.1)	7 (3.0)
	Vertical to bower to vertical	0	0	2	0	0	0	4 (2.7)	16 (6.7)
	Vertical to horizontal	0	2	2	0	0	0	5 (3.4)	19 (8.0)
Total number (% of total)		91 (63.1)	34 (23.2)	16 (10.2)	1 (0.7)	3 (2.1)	1 (0.7)	146	238

<1% of daytime at its bower (Mackay, 1989 and in Lenz, 1993). An explanation postulated for this exception is that regent bowerbirds, *Sericulus* spp., represent an early stage in the evolution of bower-building, in which bowers have not yet replaced elaborate male nuptial plumage. Male Regent Bowerbirds initiate courtship in the forest canopy, before accompanying the female to the bower where a prolonged courtship display primarily presents colourful nuptial plumage (and less so bower/decorations) to the female (Lenz, 1994). Thus the bower plays a less significant role in courtship.

It has been observed that a disproportionately large percentage of tropical rainforest-dwelling passerines, with a polygynous mating system based upon court/bower/arena displaying promiscuous males, are predominantly frugivorous. The seasonal abundance of rainforest fruits, economically undefendable because of their spatial/temporal distribution, both promotes the emancipation of males from nest duties and enables females to raise offspring unaided by conspecifics (Snow, 1976, 1982; Frith & Beehler, 1998). This said, Donaghey (1981) found that both adults and nestlings of the monogamous Green Catbird, *Ailuroedus crassirostris*, are more frugivorous than the polygynously breeding Satin Bowerbird, and noted that frugivory is but one of many factors involved in the evolution of avian promiscuity. Male Golden Bowerbirds also store, or cache, fruit foods around their bower site (Frith, 1989 & pers. obs.), as do male Macgregor's Bowerbirds (Pruett-Jones &

Pruett-Jones, 1985). Such storing of fruits around bowers would enable males to spend more time in bower attendance.

MALE BEHAVIOUR AT BOWERS. *Habitual perches, vocalisations and silence.* Bower-attending male bowerbirds studied to date advertise their bower location with specific calls given (Tooth-billed Bowerbird excepted) relatively infrequently from favoured perches (Gilliard, 1969; Veselovsky, 1978; Donaghey, 1981; Frith & Frith, unpubl. data). Male Golden Bowerbirds gave the distinctive bower advertisement *rattle*, single notes (*squeal*, *screech*, *scold-rasp* and *wolf-whistle*) and a medley of calls that included much mimicry of frog- and cicada-like notes, and fine vocal avian mimicry, from habitual perches. The Tooth-billed, Archbold's (*Archboldia papuensis*), gardener (*Amblyornis* spp.), Regent, Satin, Spotted (*Chlamydera maculata*), Western (*C. guttata*), Great, and Fawn-breasted (*C. cerviniventris*) Bowerbirds include avian mimicry in their bower advertisement and/or other non courtship vocalisations (Marshall, 1950; Gilliard, 1969; Bradley, 1987; Loffredo & Borgia, 1986; Frith, 1989; Lenz, 1993; Frith & McGuire, 1996; Frith et al., 1996, & pers. obs.). Male bowerbirds usually use a distinctly different, quieter and more complex, subsong in courtship display that, in the case of all of the above except the *Chlamydera* species, includes avian mimicry. During this study we did not hear Golden Bowerbirds giving subsong mimicry while displaying, but have done so subsequently. We

observed that long medleys of calls including much mimicry were given before/after display posturing, and particularly if a female-plumaged bird was present (see Table 7). We think it likely that this is more informative to females than advertisement song, as it has been demonstrated that female Satin Bowerbirds use the quality of more intimate male mimicry to assess the relative merits of prospective mates (Loffredo & Borgia, 1986).

Immature males lacking a bower gave medley calls with mimicry when visiting bowers, as did younger adult males in their first year of bower ownership (Frith & Frith, 2000b and this study). Adult males gave fewer medleys with mimicry, but it is possible that the quality of their avian vocal mimicry is higher than that of younger birds. Among competing male Satin Bowerbirds, older males produce longer bouts of higher-quality avian vocal mimicry than do younger males and also gain higher mating success (Loffredo & Borgia, 1986). Thorpe (1985) stated that there is some evidence that variety in male bird song is attractive to females, and suggested that mimicry may simply be a way of increasing repertoire size. Robinson & Curtis (1996) demonstrated that most mimicry content of lyrebird (*Menura* spp.) calls is learned, is culturally transmitted, and its quality and sequence (of model spp) could therefore provide conspecifics, particularly females assessing male quality, with a clear indication of potential mate experience/age/survival.

Male Golden Bowerbirds spent 80% of their time present at bower sites in perching silently above the bower, this being 9% more than in Macgregor's Bowerbird (Pruett-Jones & Pruett-Jones, 1982). While adult male Regent Bowerbirds spent only 17% of time present at the bower site in perching silently this figure merely reflects the small proportion (3%) of total daylight they spent at bowers (see above; Lenz, 1994). It would appear that male Satin Bowerbirds spent 87% of time present at the bower site in silence (Donaghey, 1981: 181-182). In marked contrast, male Tooth-billed Bowerbirds spend <2% of time perched at the court in silence, most of their time there (96%) being spent singing loudly. Court advertisement vocalisations of Tooth-bills are thus much more frequent, males having no epigamic adult plumage but a most elaborate vocal display (Frith & Frith, 1994).

Bower maintenance. Male Golden Bowerbirds spent an overall average of 4% of time at the bower site in maintaining the bower structure/

decorations. In more typical climatic conditions males spent an average of 3% of time at the bower site in bower maintenance, but during adversely dry conditions spent almost twice this time doing so. The limited time birds spent on the bower presumably reflects (a) the low maintenance required once it is largely built (given its fungus-fused and 'traditional' nature) and decorated; and (b) the fact that adult male nuptial plumage remains a predominant part of courtship in this species. Limited compatible figures for bower maintenance by: Macgregor's (12%; Pruett-Jones & Pruett-Jones, 1982), Tooth-bills (1.2%; Frith & Frith, 1994), Regent (61%; Lenz, 1994), Satin Bowerbirds (8% of all daylight; Donaghey, 1981) are variable. The figure for Tooth-bills is so low because males spend so much of daylight above the court (but at its site); whereas the high figure for the Regent, which builds a most rudimentary and sparsely-decorated bower, is because males spend little time at the bower site (Lenz, 1994).

In restricting its decorations to beard lichen, melicope seed pods and whitish flowers, the Golden Bowerbird is far less catholic in bower decorations than all other polygynous bowerbirds with the exception of the Tooth-bill which uses only leaves of various plants (Frith & Frith, 1993, 1994) and the Fawn-breasted Bowerbird which uses only green fruits, leaves and the occasional flower (Peckover, 1970; Pruett-Jones & Pruett-Jones, 1994). Bower decorations of greater significance to some bowerbird species are items rare in the birds' environment (Frith & Frith, 1990c; Frith et al., 1996), and an abundance of such decorations on bowers enhances the mating success of the bower owner (Borgia, 1985b, 1986; Borgia & Gore, 1986). Thus, rare decorations might indicate something significant to females, and rival males, about the owner's fitness/dominance levels. But are bower decorations used by Golden Bowerbirds rare in their habitat? The answer needs to be framed in the context of extensive undisturbed upland rain-forest, lacking the roads, tracks and clearings of today. In this context, we suggest that melicope seed pods would have been relatively hard to find, as *M. broadbentiana* is a pioneer shrub (Hyland & Whiffin, 1993) that is today found on track/clearing edges. Before the latter were available the plant would have been largely confined to areas of small-scale natural forest damage, such as larger tree falls and cyclones.

While beard lichen is far more widespread in upland forest than the melicope it is sun-loving

and would, in extensive primary upland forest, have been predominantly confined to woody twigs and branches of upper canopy and emergent trees — an exposed part of the forest not typically frequented by Golden Bowerbirds (pers. obs.). Fresh orchid flowers are never spatio-temporally abundant in Australian upland rainforest and in any event, like the whitish flowers of other plants, provide inferior bower decorations because they wilt and need replacement. Golden Bowerbirds can thus be seen to fit the broad pattern of male bowerbirds using some items that are relatively rare as bower decorations.

Adult males briefly visited the bower of rival males, usually in their absence, in order to steal bower decorations. Such decoration theft has been documented for several other bowerbirds; including the Tooth-billed (Frith & Frith, 1993, 1994), Vogelkop (Diamond, 1986a,b, 1987, 1988), Regent (Lenz, 1994), Satin (Borgia 1985b; Borgia & Gore 1986; Hunter & Dwyer, 1997), Fawn-breasted (Coates, 1990) and Yellow-breasted (*C. lauterbachii*) Bowerbirds (Pruett-Jones & Pruett-Jones, 1994).

Bower marauding is known in Macgregor's, Vogelkop, Regent, Satin, Spotted, Fawn-breasted and Yellow-breasted Bowerbirds (Pruett-Jones & Pruett-Jones, 1994). While male Golden Bowerbirds may (but not observed) steal the odd, unfused (i.e. recently placed), stick from the bower apex of a rival male, we did not see any attempt to damage ('maraud' of Pruett-Jones & Pruett-Jones 1994: 609) a bower of a rival. Bower-owning male Macgregor's Bowerbirds attempt to damage bowers of rivals as well as steal their decorations, including the moss of the tower base (Bulmer in Gilliard, 1969: 305; Pruett-Jones and Pruett-Jones, 1982; pers. obs.). Stealing of the latter is noteworthy, suggesting it may function as decoration (analogous to beard lichen on Golden Bowerbird bowers) and not a structural element.

It has been demonstrated that a strategy of bower decoration theft by males is an evolutionarily stable one, as opposed to the contrary strategy of guarding bowers and not stealing (Pruett-Jones & Pruett-Jones, 1994). Male Satin Bowerbirds with more decorations on bowers tend to steal more often than they are stolen from (Borgia & Gore, 1986). This is because relative levels of bower decoration enable females to assess an individual male's quality (fitness), based upon his success in conflict with rival males. The greater numbers of more favoured

decorations on a bower positively influenced relative male mating success (Borgia, 1985a,b, 1986; Borgia et al., 1985; Pruett-Jones & Pruett-Jones, 1994). Bower quality has also been found to correlate well with relative male mating success in both Satin and Regent Bowerbirds; and males of both species mostly maraud and damage bowers of their nearest neighbours, their most likely sexual competitors (Borgia, 1986; Lenz, 1993). The reason for theft by rival males is thought to be sexual selection resulting from females choosing to mate only with males 'honestly advertising' their fitness with such 'rare' bower decorations (cf. Zahavi & Zahavi, 1997).

Displacement chases and displays. As 81% of all female-plumaged conspecifics perching on the bower were immediately displaced and aggressively pursued out of the bower site by the bower-owning male Golden Bowerbirds it is likely, in view of what is known of other bowerbirds, that such behaviour typically greets females as well as adult and immature males. Of the 19% of visiting female-plumaged birds not immediately chased off, half were displayed to and half ignored. Adult males displaced and chased immature and adult males from their bower/site but we only twice saw physical combat, as did Chisholm & Chaffer (1956).

Display by a male concealing himself from a visiting female, by crouching behind a court tree or central maypole bower base to give subsong with mimicry, is typical initial Tooth-billed, Macgregor's and Streaked (*Amblyornis subalaris*) Bowerbird courtship (Diczbalis, 1968; Gilliard, 1969; Frith & Frith, 1993 & pers. obs.). We saw no male Golden Bowerbird attempting to hide from a visiting female to give subsong with mimicry during this study, but have subsequently done so. In hindsight, we understand this was due to limited field of view from hides, a point of great importance to students of bowerbird behaviour (Frith & Frith, unpubl. data).

It is probable that the three basic display elements we observed are performed during successful courtship, perhaps in a typical progressive sequence, but as we witnessed few displays to (unsexed) female-plumaged birds ($n = 26$), and no copulations, we could not confirm this. The *Head nod and shake* display is only broadly similar to postures and movements known to be performed by courting male Gardener and Archbold's bowerbirds (Gilliard, 1969; Frith et al., 1996; pers. obs.). The *Bow* display, which enhances the contrastingly

brilliant yellow mid-crown patch and nape 'crest', appears unrecorded in other bowerbirds.

The *Flight/hover* display is unique to the Golden Bowerbird. This is not surprising, as this display clearly functions to visually present both the (uniquely within Ptilonorhynchidae) brilliantly coloured dorsal and ventral contour and flight plumage of adult males. The deliberate slow flight display punctuated with hover(s) with conspicuously repeated tail-fanning, to expose the pure yellow outer rectrices, is visually spectacular. This might be performed with a bower decoration held in the bill (Chaffer in Chisholm & Chaffer, 1956; and this study). The closest any other bowerbird comes to a courtship flight display is the vigorously repeated to-and-fro 'extra-bower' fluttering flight/leaps, between vertical sapling stems, by closely related Maegregor's Bowerbird (Stevens in Greenway, 1935; Mackay & Cheeseman, 1990; pers. obs.). It has been noted that bowers of Maegregor's Bowerbird are often built adjacent to numbers of vertical sapling trunks (Gilliard, 1969: 302; Pruett-Jones and Pruett-Jones, 1982), and they might be a prerequisite bower site feature to accommodate the 'flight' display. In the light of this, and in view of the elements of its *Flight/hover* display, it is possible saplings appropriate for hovering at/perching on might influence bower site selection by Golden Bowerbirds.

Male Golden Bowerbird behaviour at bower sites is mostly cryptic, given they are displacement chasing and/or displaying for <2% of their total time present there. Males apparently depends largely upon bower/decorations and, subsequently, their colourful plumage to impress females, rather than a complex bower. Thus, it has been observed that in this bowerbird, unlike most, untidy bower construction and variation in their shape/bulk suggests gross bower features are of less significance to females than is the discrete and relative small part of them modified into a 'platform(s)' for the exclusive placement of decorations (Frith & Frith, 2000a). Maintenance and decoration of the platform(s) requires but a small proportion of bower attendance time, once the basic bower is accumulated. The platform(s) does, however, provide a quickly and easily located 'marker' (cf. Borgia, 1985a; Borgia et al., 1985) for females seeking older, more experienced, males to assess as potential mates.

No data were obtained on relative reproductive success rates within male Golden Bowerbird populations. The possibility that older males are

more successful than younger rivals has been found, or indicated, to be the case in other non-lekking bowerbirds (Borgia, 1985a) and in unrelated lekking passerines in which promiscuous males court females at traditional sites (Lill, 1974a,b; McDonald, 1989a,b; Andersson, 1991). Clearly, promiscuous adult males establishing themselves within a lek, exploded lek or more dispersed population, enjoy a high survivorship (Frith & Frith, unpubl. data). Evidence from sexually dimorphic polygynous bowerbirds, and other species, suggests that the strong mating skew in favour of older individuals has forced males into a long-term mating strategy involving much-delayed morphological and physiological development (Beehler & Foster, 1988; Collis & Borgia, 1992; Frith & Beehler, 1998).

Bower site ownership by Golden Bowerbirds is highly stable over years, with few successful attempts by newcomer (predominantly younger) males to establish themselves within bower-owning male society. Given this scenario, and that experience/age has been found to play a highly significant role in relative male bowerbird mating success (Loffredo & Borgia, 1986; Collis & Borgia, 1992; Borgia, 1995), there is a high expectancy of the latter within local male Golden Bowerbird populations. This remains to be tested.

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